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FRUIT DIVERSITY AND DISPERSAL IN *SOLANUM* IN AUSTRALIA

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Abstract

The forms of fruits of the Australian species of *Solanum* are described and related to their dispersal agents. The succulent berry is the most common, but trample burrs, censer mechanism, capsules, hard and dry berries and a possible tumble weed have evolved. Birds are the most commonly recorded agent of dispersal but marsupials, wild dog, bats, man, wind and water are important.

Introduction

The genus *Solanum,* with about 90 species native to Australia, has evolved a range of fruits and dispersal mechanisms. The growth habits of the native species vary from annuals to small trees, the most common being herbaceous perennials or small to medium, colonial, short-lived shrubs. The fruits of *Solanum* are typically described as berries (pulpy indehiscent fruits with seeds embedded in the flesh) but several modifications have evolved and succulent berries, finally-dry bony fruits, trample burrs, capsules, censer mechanisms and several variations less easily classified may be found.

This account has been influenced by the systematic account of dispersal by Van der Pijl (1969) who discusses many aspects of the biology involved, and the agents responsible for dispersal and the syndromes of plant characters that may be associated with each. Classification of fruits into a single category is not always possible, particularly for succulent fruits produced close to the ground which may be taken by reptiles, birds or mammals.

The types of fruits of Australian *Solanum* species and their likely means of dispersal are shown in Table I.

Dispersal by reptiles: Saurochory

The syndrome of fruit characters that Van der Pijl associates with saurochory is that fruits may be coloured, have a smell and often borne near the ground or dropped at maturity. It is obviously not an exclusive group of characters and fruits with them are also likely to be distributed by birds and mammals.

The large omnivorous skinks, e.g. Sleepy Lizard *(Trachydosaurus rugosus),* Blue Tongue *(Tiliqua scincoides)* and Spiny Skink *(Egernia stokesii)* are widespread across semi-arid southern Australia. The first is known to be partial to cultivated strawberries and tomatoes and both Sleepy and Blue Tongue Lizards have been found in the vicinity of *S.simile* which has drab green (sometimes purplish), succulent, aromatic fruit which drops to the ground when ripe. Other species with similar fruits include *S.opacum, S.vescum, S.cleistogamum, S.ellipticum, S.pungetium, S.prinophyllum.*

Species with coloured fruits that drop to the ground but which grow in mesic and/or tropical sites are beyond the geographical range of these lizards. These species include *S.discolor* which has erect and prostrate growth forms and the taller *S.macoorai, S.laciniatum* and *S.aviculare.* The fruits of the last three species are known to be eaten by birds.

Dispersal by birds : Ornithochory

The fruit characters associated with dispersal by birds are:- an attractive edible part when ripe, outer protection against premature eating and signal colours at maturity. There is less emphasis on aroma and strength of attachment, and no special placement on the plant. Neither reptiles nor birds (except Cockatoo) can usually cope with a hard rind.

Table 1. The fruit types of Australian *Solanum* species.

Fruit type	Number of species	Likely means of dispersal
Succulent, red, orange, yellow berries *S. aviculare* Forst.f., *chenopodinum* F. Muell., *defensum* F. Muell., *densevestitum* F. Muell., *discolor* R.Br., *dunalianum* Gaud., *elegans* Dun., *ferocissimum* Lindl., *ferox* L., *inaequilaterum* Domin, *laciniatum* Ait., *linearifolium* Gerasimenko, *macoorai* Bailey, *nemophilum* F. Muell., *parvifolium* R.Br., *stelligerum* Sm., *tetrandrum* R.Br., *viride* R.Br., sp.nov. (yirrkalensis ms.)[1]	19	birds
Succulent, black berries *S.americanum* Mill., *semiarmatum* F.Muell.	2	birds
Succulent, drab green berries *S.capsiciforme* (Domin) Baylis, *cleistogamum* Symon, *dianthophorum* Dun., *ellipticum* R.Br., *hoplopetalum* Bitt. & Summerh., *horridum* Dun., *hystrix* R.Br., *multiglochidiatum* Domin, *opacum* A.Br. & Bouché, *prinophyllum* Dun., *pungetium* R.Br., *simile* F.Muell., *symonii* Hj. Eichler, *vescum* F.Muell., sp.nov. (terraneum ms.)	15	lizards and birds
Firm, greenish berries *S.dallachii* Benth., *dimorphospinum* C.T. White, *furfuraceum* R.Br., *hamulosum* C.T. White	4	mammals and birds
Firm, yellowish berries		
1) large, 2-4 cm diam. *S.campanulatum* R.Br., *cunninghamii* Benth., *dioicum* W.V. Fitz., *diversiflorum* F.Muell., *eburneum* Symon, *melanospermum* F. Muell., *vansittartensis* Gardner, sp.nov. (beaugleholei ms.) sp.nov. (clarkiae ms.) sp.nov, (chippendalei ms.)	10	mammals and birds
2) small, 1-2cm diam. *S.adenophorum* F.Muell., *brownii* Dun., *centrale* J.M. Black, *coactiliferum* J.M.Black, *elachophyllum* F.Muell., *eremophilum* F.Muell., *esuriale* Lindl., *lacunarium* F.Muell., *nummularium* S. Moore, *orbiculatum* Dun., *oldfieldii* F.Muell., *papaverifolium* Symon, *tetrathecum* F.Muell., *tumulicola* Symon, sp. nov. (cookii ms.) sp.nov. (hesperium ms.) sp.nov. (plicatile ms.)	17	mammals and birds
Firm, yellowish, finally hard and bony and often enclosed in a prickly calyx. *S.gilesii* Symon, *karsensis* Symon, *lachnophyllum* Symon, *lasiophyllum* Dun., *oligacanthum* F.Muell., *petrophilum* F.Muell., *quadriloculatum* F.Muell, sp.nov. (ashbyae ms.) sp.nov. (eardleyae ms.), sp.nov. (petraeum ms.)	10	? mammals
Trample burrs (berry enclosed in prickly calyx) *S.asymmetriphyllum* Specht, *echinatum* R.Br., *gabrielae* Domin, *leopoldensis* Symon, *lucani* F.Muell., sp.nov. (scitheae ms.)	6	feet of mammals
Finally dry, parchment balloon form *S.cinereum* R.Br.,	1	?wind, wash

Tumble weed *S.pugiunculiferum* C.T. White	1	wind
Finally dry, censer mechanism sp.nov. (tudununggae ms.)	1	wind
Finally dry, fracturing *S.oedipus* Symon, *sturtianum* F.Muell., sp.nov. (heteropodium ms.)	3	?
Unknown *S.carduiforme* F.Muell., *cataphractum* A.Cunn. ex Benth.	2	—

[1] New species combinations to be published by Symon (in preparation).

In a number of the following records it is not clear whether the birds are agents of dispersal as well as predators. The ability of birds to grind up ingested food varies greatly and a record that a bird eats a fruit does not mean that viable seeds are passed in the faeces.

All immature *Solanum* fruits are green or striped green and so are cryptically coloured. Many are also extremely bitter, containing higher amounts of alkaloids when green than when ripe, Collins (1976). The fruits of the species which are dispersed by birds change from green to orange, red or black on ripening and become succulent. A few are noticeably aromatic and none have a hard rind or prickly calyx. *S.americanum* (related to Black Nightshade,**S. nigrum* L., known to be eaten and distributed by birds), and *S.semiarmatum,* also with shiny black fruits, belong to this group.

Cleland (1918) records that the Stubble Quail *(Coturnix novaezelandiae),* Silver Eye *(Zosterops lateralis)* and the Lewin Honeyeater *(Meliphaga lewinii)* all eat fruits of the alien **S. nigrum.* Griffiths (1977) reports that the Mistletoe-bird *(Dicaeum hirundinaceum)* will also feed on the berries of this species. Barker in Frith (1976) reports that the Stubble Quail in south-eastern Australia frequently contains minor amounts of unidentified *Solanum* seeds.

The ravages of birds have been seen on *S.laciniatum* which has succulent orange-yellow fruits. Paton (1976) reports that Silver Eyes *(Zosterops lateralis)* and Yellow Faced Honeyeaters *(Lichenostomus chrysops)* reduce the fruits to empty skins while still on the bush. The author has noted that birds eat *S. aviculare,* **S. erianthum* Don, and **S. mauritianum* Scop. and *S. linearifolium* (Fig. 1, no.5) probably belongs here also.

Tropical pigeons are known to eat the fruits of several species of *Solanum.* Lea & Gray (1935) recorded that Wonga Pigeons *(Leucosarcia melanoleuca)* ate unidentified *Solanum* berries at Imbil, Queensland. Frith & Barker (1975) recorded unidentified *Solanum* seeds in two Plumed Pigeons *(Geophaps p. plumifera* and *G.p.ferruginea)* in arid north western Australia. In all cases the number of seeds collected was quite low. Frith (1976) records the Banded Pigeon *(Ptilinopus cinctus)* eating fruits of the alien **S. mauritianum* and it is probable that fruits of the closely related **S. erianthum* would also be eaten. Crome (1975) working in tropical, lowland rainforest 50 km south of Innisfail, Queensland found that the frugivorous Brown Pigeon *(Macropygia amboinensis)* ate *Solanum* fruits and that berries of the weedy, alien species **S. torvum* Swartz were a consistently important food source. Its fruits, which are greenish or greenish-yellow, were available over a longer period of time than any of the other 55 food plant species recorded. The Brown Pigeon was the only one of the seven pigeons investigated that was found to contain *Solanum* fruits. Fruit was always taken from the crown of the trees and fallen fruit was never seen to be taken. *S. viride* with succulent, red fruit was also a minor component of diet.

* Introduced species.

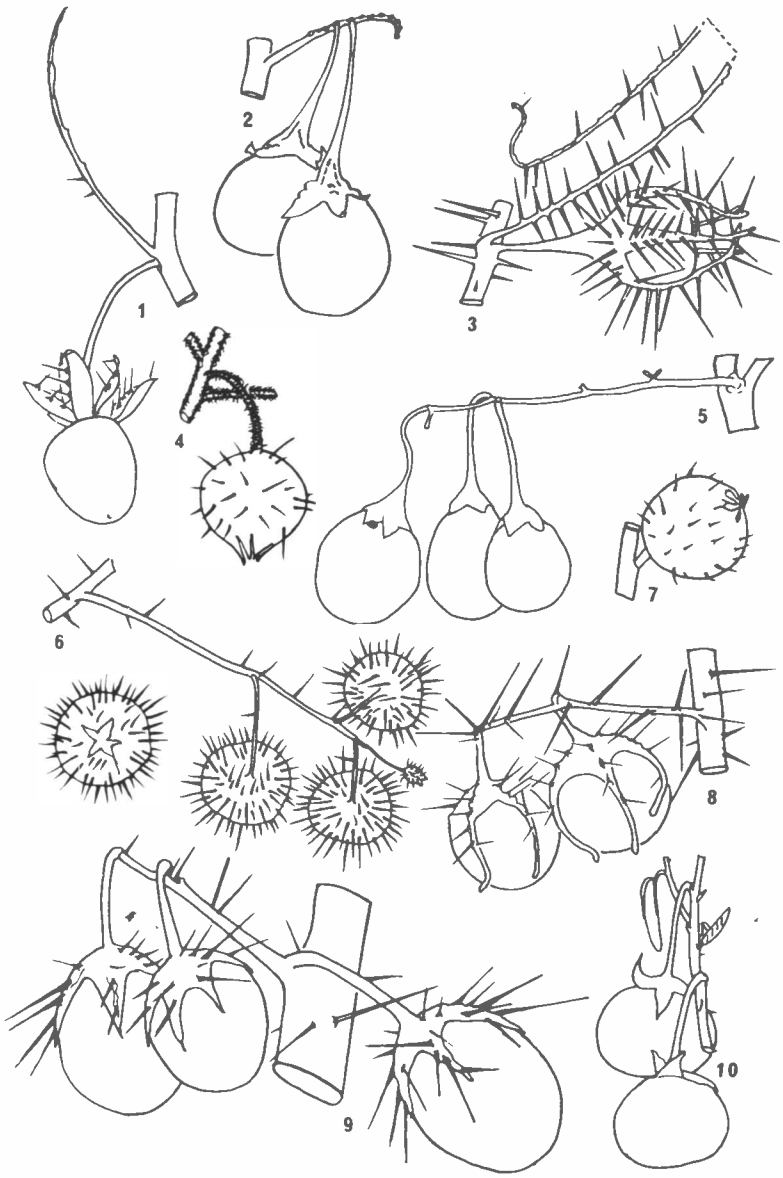

Fig. 1. Drawings of selected Australian *Solanum* fruits, about natural size, the lower four x 1.5.

1. *Solanum melanospermum:* Large yellow berry, prickly calyx reflexed when ripe.
2. *S. dallachii:* Firm green fruit, shed when mature.
3. *S. oedipus* Green, scarcely fleshy, finally sub-capsular.
4. *S. gilesii:* Greenish fruit, finally firm, enclosed in calyx.
5. *S. linearifolium:* Succulent ochre-yellow fruit.
6. *S. echinatum:* Trample burr; firm, greenish berry enclosed in calyx.
7. *S.* sp.nov. Subcapsular berry remaining enclosed in calyx.
8. *S. petrophilum:* Firm yellowish fruit, finally pale and bony.
9. *S. cinereum:* Firm yellowish fruit, finally parchment like balloon.
10. *S. coactiliferum:* Firm yellowish fruit.

Two Aboriginal inhabitants from Yirrkala, Rita Baakili Gurruwuwuy and Margaret Djwanydangu Yunupingu have reported through Scarlett (1976) that two pigeons, Laparr, Green Winged Pigeon *(Chalcophaps chrysochlora)* and Jukuk, Peaceful Dove *(Goepelia placida)* feed on the red fruits of a new species of *Solanum* from Yirrkala, Arnhem Land.

Crome (1976a) in an account of the breeding and feeding of the Torres Strait Pigeon *(Myristicivora spilorrhoea)* at the Low Isles (N.E. Queensland) reports that **S. torvum* and **S. mauritianum* were both eaten and excreted by the birds. Both these are alien species and the observations add significance to the importance of frugivorous pigeons as dispersal agents of *Solanum* in these tropics. Some species with succulent red fruits which are probably eaten by birds include *S. stelligerum, S. densevestitum, S. tetrandrum* and *S. parvifolium.*

There are few records of parrots eating *Solanum* fruits. Lea & Gray (1935) report that the Rainbow Lorikeet *(Trichoglossus moluccanus)* from Encounter Bay, South Australia, contained unidentified *Solanum* seeds and the Mallee Ringneck *(Barnardius barnardi)* from Mannum, South Australia contained "many larger yellow seeds of a *Solanum* species". The Adelaide Rosella *(Platycercus elegans)* from Mt Remarkable, South Australia, contained seeds of an unidentified *Solanum* and a bird from Second Valley, South Austrlaia, contained seeds of **S. nigrum.*

In Australia the Emu *(Dromaius novaehollandiae)* probably deserves special consideration as an agent of dispersal. It is a large, omnivorous, flightless bird once found widely throughout Australia. It is known to eat almost any flower or fruit it can swallow, including the spiny aggregate fruits of *Dissocarpus paradoxa* (R.Br.) F.Muell. Innumerable seeds and bony endocarps of *Acacia, Eremophila, Nitraria, Myoporum, Santalum, Leucopogon* etc. may be found in its faeces. It is probable that Emus eat a wide range of *Solanum* fruits. I have seen them eating the succulent green and aromatic berries of *S.ellipticum* which are produced at ground level below the leaves. The birds probed around the base of the plants and after seizing a fruit raised their heads to swallow it. Faeces collected at the time contained entire fruits with intact prickly calyx and pedicel as well as seeds. Examination of three faeces samples showed the presence of 2,000, 2,800 and 7,000 seeds or remnants, some of which appeared to be sound.

Noble (1975) records that in some months *S.esuriale* may constitute up to 25% (dry weight) of the diet of Emus on the riverine plain of New South Wales. No comment is made on the condition of the seeds passed in faeces but some could be expected to be viable. Latz (1976) records that Emus in an area near Tanami, Northern Territory, ate "copious quantities" of *S.centrale* and *S.gilesii.* It is not surprising that *S.centrale* is eaten as the berry is exposed and known to be palatable. The berry of *S.gilesii* is covered by a prickly calyx which is obviously an inadequate deterrant in this case. Almost any *Solanum* fruit produced between ground level and 2m would be accessible to Emus as well as any fruits that are shed. It is now obvious that there is not likely to be much distinction between the fruits eaten by reptiles and Emus and indeed many of the other categories.

Australia's second large, flightless bird is the Cassowary *(Casuarius casuarius)* which, unlike the widespread Emu, is narrowly confined to tropical scrubs and rainforests of northern Queensland. Crome (1976b) reports them to be omnivorous fruit eaters. In particular they eat fallen fruit and occasionally fruit from branches. Usually the pericarp of the fruit is digested and the seeds are excreted whole. He reports finding **S.torvum* in their faeces and Hyland (1976) reports that the large reddish fruits of *S.macoorai* occur in their droppings near Atherton. In view of Crome's observations on their habit of eating fallen fruit it is likely that they may be one agent distributing the seeds of other *Solanum* species. In the area there are four tall or scrambling species that produce yellow/orange/green fruits of moderate size (1-2 cm diam.) which may fall when ripe, including *S.dallachii* (Fig. 1, no.2) and *S.hamulosum.* As Jansen (1975) points out, the mere release of fruits from the parent

plant may not constitute dispersal. Seeds on the ground beneath the parent tree are very likely to be undispersed seed. Seedlings developing close to the parent may result in intense conspecific competition particularly among perennials. It is probable that fruits released on to the ground are placed within the reach of some dispersal agent, in this case the Cassowary. It is noteworthy that at least a dozen varied *Solanum* species shed their fruits, usually with their pedicels, when ripe in Australia.

Dispersal by mammals : Mammaliochory

Adaptive mammaliochory of fruits is perhaps not so readily detected. Van der Pijl considers that a firm skin is less of an impediment to consumption, and some protection of the seed proper against mechanical destruction could be expected. Aroma may attract the animals and fruits are often of larger size and have to be accessible. As many Australian marsupials are night feeders (or at least dawn and dusk), or are arboreal, fruit colour may be less important.

It will be seen from Table 1 that the largest single category of fruits in Australian *Solanum* is that with firmish yellow fruits, all of which are produced on small shrubs up to 2m high. These species fall into two sub-groups, one with medium sized (1-2cm diam.) exposed fruits with pale seeds, e.g. *S. esuriale,* and a second group with larger fruits (2-4cm diam.) partially enclosed in prickly calyces. The latter have black seeds. In northern Australia the species in the second sub-group have larger fruits protected by prickly calyces which relax or reflex to expose the fruits when ripe. These fruits may be held along or below the branches and do not normally seem to drop off. Examples are *S.phlomoides, S.eburneum, S.melanospermum* (Fig.1, no.1), *S. dioicum* and *S. cunninghamii.*

Van der Pijl pleads for information on the relations between diaspores and kangaroos in Australia. Normally the larger kangaroos and wallabies eat grass, herbs and foliage and are not fruit-eaters. I have seen evidence on Eyre Peninsula of kangaroos eating the fruits of *S. coactiliferum,* (Fig.1, no.10). This is a small shrub with unarmed, firm, yellowish fruits. It is widespread in southern Australia with a suite of about 15 related species including *S. esuriale, S. tetrathecum, S. oldfieldii, S. orbiculatum.* However many of these would be accessible to both reptiles and birds. Cleland and Tindale (1954) briefly describe *S. quadriloculatum,* a species with a firm yellow fruit finally becoming hard and bony, as "kangaroo food, not used by the natives" and *S. ellipticum,* with succulent green fruit at ground level, as "eaten by euros and wallabies". Newsome (1976) has recorded the Red Kangaroo *(Megaleia rufa)* eating *S. ellipticum* in Central Australia. Waring (1976) reports that the Quokka *(Setonix brachyurus),* a small wallaby, eats *S. simile* in W. Australia.

Despite the widespread occurrence of possums in Australia and their frugivorous/herbivorous diet the only records of their consumption of *Solanum* is a report by Martin (1969) that they eat the fruit of *S. vescum* in Tasmania.

The Wild Dog, Dingo *(Canis familiaris dingo),* like the Emu, was once widespread in Australia both wild and semi-domesticated by the Aborigines. Dingoes are basically carnivorous but include large insects and fruits in their diet. Finlayson (1943, p. 142) says of the dingo, "in virgin country a mixed feeder, depending partly on fruits (especially those of the numerous *Solanum)".* Unfortunately no species names are given. Newsome (1976) has found the seeds of *S. vescum* to be common in their faeces at Nadgee (S-E of N.S.W.) and it is probable that allied species such as *S. simile, S. laciniatum, S. aviculare, S. linearifolium* (Fig.1, no.5) were also eaten. It is possible that dingoes may occasionally eat fruits of a wide range of species that are within reach or shed on the ground. In addition Newsome also found seeds of *S. vescum* in faeces of the introduced European Fox *(Vulpes vulpes).*

The Flying Foxes *(Pteropus* spp.) are widespread in tropical Australia and feed on blossoms and various fruits, usually well above the ground in trees. Ratcliffe (1931) found that they fed on "Wild tobacco *Solanum* sp., a tall herb, profuse in cleared rain forest area".

This is most probably **S. mauritianum* which is now abundant as a weedy, small tree, but could also include **S. erianthum*. Both of these species are introductions to Australia, **S. erianthum* before white settlement and **S. mauritianum* later. Both come from Central America and their dispersal agents there would be of interest. Because of their delicate wing membrane it is perhaps unlikely that bats scrabble about the more prickly solanums which in any case do not present their fruits conveniently to them.

Transport on the surface of animals : Epizoochory

Fruits dispersed on the surface of animals may have adhesive mechanisms such as spines, hooks or viscid exudates. This category has been exploited in *Solanum* by the production of trample burrs in some six species. The berries of *S. echinatum* (Fig.1, no.6) and *S. lucani* are relatively small and surrounded by densely prickly calyces. The berries are produced at ground level and are shed *(S. echinatum)* or readily broken off *(S. lucani)* when ripe. *S. gabrielae* sheds larger globular, viscid and prickly fruits from a small shrub, and *S. leopoldensis* sheds bony berries partially enclosed in a raised prickly calyx. It is no coincidence that all of these species occur on rocky outcrops and defiles favoured by wallabies.

The somewhat larger, less prickly fruits of *S. asymmetriphyllum* may also belong here, but there seem scarcely enough prickles to attach this fruit to a passing foot. It too grows on rocky sites. Van der Pijl points out that burry fruits may also serve as anchoring mechanisms to facilitate germination and establishment, but as each of these berries may contain several hundred seeds, seedling competition could be intense and they are in marked contrast to the few seeds present in the classical trample burrs such as *Emex* or *Tribulus*.

Man as a dispersal agent : Anthropochory

The Australian Aborigines are food gatherers and do not practice agriculture. A number of *Solanum* species are gathered and eaten by them. I do not know if viable seeds are found in their faeces. However, the gathering, transport and consumption of fruit would certainly have resulted in dispersal of seeds. The fruits of *S. chippendalei* (large, firm, yellow) are popular and seeds scraped out before the fleshy part is eaten (Gould, 1969). In addition *S. ellipticum, S. cleistogamum* and particularly *S. centrale* are popular with the central Australian Aborigines and are consumed in large amounts. Records of *Solanum* eaten in southern Australia are meagre but *S. esuriale* (Mitchell, 1839), *S. vescum* (Mueller, 1855), *S. laciniatum* (Roth, 1899), and *S. simile* (Richards, 1882) are known to have been eaten. All of these species have succulent yellowish or greenish fruit. I have found no record of the consumption of *Solanum* in the high rainfall tropics and Specht (1958) does not include any species in his account of the ethnobotany of Arnhem Land. Latz (1976) reports that Aborigines near Tanami, Northern Territory eat *S. gilesii* which at first glance does not appear to be an attractive species. Wherever the fruits were handled or eaten the seeds were likely to be discarded in the vicinity of camps and to be in the disturbed sites frequently occupied by *Solanum*. For a summary of the Aboriginal consumption of Solanaceae see Peterson (1976).

Modern man has been an active agent in transporting native species to new sites. *S. aviculare* and *S. laciniatum* have become established in Eyre Peninsula, South Australia and also in Western Australia, most likely as garden escapes. *S. cinereum* from N.S.W. is now established in South Australia. *S. capsiciforme, S. oligacanthum* and *S. sturtianum* have all been found far from their original areas of establishment, the last two along railway lines suggesting transport by stock.

Wind dispersal : Anemochory

Many wind dispersed fruits and seeds are known; Van der Pijl lists flyers, rollers and throwers.

Fig. 2. *Solanum* sp.nov. (S. tudununggae ms ined) showing the fruits held high on a willowy stem, Kalumburu, W. Aust.

The unique, as yet unnamed *Solanum* from Kalumburu (Kimberleys, W.Aust.) may be a wind ballist. This species is tall and slender (to 2m) and is sparsely branched. The fruits are firmly held to the stem by tough pedicels. The berry is enclosed, except for a small orifice, by a firm globular calyx. The berry within, which is broadly attached, is circumcissile at its base and when shed shrinks to form a loose cap within the calyx. The seeds are then released through the orifice of the calyx when the stem is knocked, shaken or blown (a censer mechanism). I know of no other species like this in the genus (Fig.1, no.7; Fig.2).

The species *S. sturtianum* may be a less specialised wind ballist. The berries at first firm and yellowish, are held erect on short pedicels on a shrub 0.5-2 m tall. The berries are finally almost black with a brittle, dry skin. The relatively large dark seeds drop out or can be knocked out when the fragile skin breaks, and could belong to one of Van der Pijl's last group — barochory — seeds dispersed by weight. A somewhat similar small group of 4 species from the Kimberleys includes *S. oedipus* (Fig.1, no.3) and *S. heteropodium.* Their berries are initially green, not fleshy and enclosed in very prickly calyx lobes. The lobes eventually spread widely and the scarcely succulent fruit containing relatively large dark seeds disappears. The agents are not known, but like the new species mentioned above, the berry is very broadly attached to the calyx and it is difficult to remove the ripe berry as an intact unit.

S. pugiunculiferum is possibly a tumble weed although the plants have not been seen in motion. This is an annual species (very rare in Australian *Solanum)* and it grows in northern Australia on flats of heavy, cracking clays following seasonal flooding. The plants are very prickly, somewhat rounded in form, the berries small, firm, green and the seeds flat and papery.

A possible wind ballist of the balloon type is the berry of *S. cinereum* (Fig.1, no.9). These large yellowish berries finally dry to form a brittle parchment-like sphere with the seeds adherent to the placenta; at this stage they have the smell of dried fruit, (dried litchi). The spheres are not readily freed from the pedicels and their method of dispersal is obscure.

Other methods of dispersal

A group of about eight species has firm yellowish berries that finally become hard, pale and bony at maturity. They are often enclosed in a prickly calyx. There is no dehiscence and the fruits remain on the bushes for long periods. Examples are *S. petrophilum* (Fig.1, no.8) and *S. quadriloculatum,* both of which have long prickly calyx lobes enclosing the berries and *S. gilesii* (Fig.1, no.4), *S. lachnophyllum* and *S. lasiophyllum* which have their berries enclosed in a prickly calyx tube. The means of dispersal are obscure though *S. quadriloculatum* at least may be eaten by Kangaroos (Cleland & Tindale, 1954). However it is also possible that after the short-lived plants have collapsed the intact fruits may be blown, washed or trampled to new sites.

No dispersal by ants, fish or rodents have been recorded, nor are examples of plumose, winged flyers or active ballists known in Australian *Solanum.*

It is of interest to compare dispersal of fruits of *Solanum* in Australia with that on a cross section of *Solanum* species described by D'Arcy (1973) and Gentry & Standley (1974) in Panama and Guatemala. A total of 93 species are dealt with by D'Arcy and Gentry and Standley, of which 85 have adequate descriptions of the fruit for comparison to be made. Most of the fruits are globose or ovoid, but two species have fruits described as flat or lance shaped, a form not present in Australia. Conspicuously pubescent fruits occur in 10 species. This characteristic is almost absent in Australia; only *S. ferox* is conspicuously pubescent and this species is localised and probably a recent introduction. Two sparsely pubescent species here, **S. erianthum* and **S. mauritianum,* are both of American origin. The most common fruit colours present were red/orange/yellow (34 species), purple/black (19 species), green (12 species), white (4 species — not present in Australian species) and 24 species had no colour specified. A conspicuous difference between the two areas is the number of species in Australia with fruits enclosed in often very prickly calyces. In Australia there are at least 15 such species in contrast to two in Panama-Guatemala. The distribution in Australia of species with berries enclosed in calyces is predominantly in the arid and monsoonal areas with relatively open vegetation forms. None are found in the high rainfall or rainforest areas of eastern Australia. No *Solanum* fruits from Panama-Guatemala appear to be capsular (with the exception of the introduced *S. cornutum),* and none have finally hard bony berries. In Australia the former are mainly in the monsoonal tropics and the latter essentially in the arid areas.

Concluding remarks

Although factual records of dispersal are not abundant it can be seen that a wide range of agents are involved and that the 'berry' of *Solanum* has been subject to considerable diversification and adaptation.

The species of *Solanum* in Australia are grouped by Symon (in preparation) in a number of subgenera which have not been elaborated here. In the subgenus *Archaesolanum,* Kangaroo Apples, all seven species have typical succulent berries as do the few examples of subgenus *Solanum,* Black Nightshade. Greatest diversity of fruit form occurs in the prickly stellate-haired subgenera and within these the andromonoecious and androdioecious species (concentrated mainly in northern and especially north western Australia) show most variation. It is of interest that in the relatively large group of tuber-bearing species (about 200) in the Americas, nothing like the Australian range of fruit form occurs. Nor in the smaller Black Nightshade subgenus *Solanum* (perhaps 50 species) does there appear to be much variety of fruit form. The subgenus *Brevantherum,* of about 27 species mainly in Central America, also has relatively uniform succulent berries. In many of the older and even recent accounts, the descriptions of *Solanum* fruits are inadequate, no doubt due to the fact that a pressed succulent berry makes a mouldy mess whose structure is difficult to measure and describe.

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